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Multiple facets of biodiversity drive the diversity-stability relationship

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A significant body of evidence has demonstrated that biodiversity stabilizes ecosystem functioning over time in grassland ecosystems. However, the relative importance of different facets of biodiversity underlying the diversity-stability relationship remains unclear. Here we used data from 39 grassland biodiversity experiments and structural equation modeling to investigate the roles of species richness, phylogenetic diversity, and both the diversity and community-weighted mean of functional traits representing the 'fast-slow' leaf economics spectrum in driving the diversity-stability relationship. We found that high species richness and phylogenetic diversity stabilize biomass production via enhanced asynchrony in the performance of co-occurring species. Contrary to expectations, low phylogenetic diversity enhances ecosystem stability directly, albeit weakly. While the diversity of fast-slow functional traits has a weak effect on ecosystem stability, communities dominated by slow species enhance ecosystem stability by increasing mean biomass production relative to the standard deviation of biomass over time. Our in-depth, integrative assessment of factors influencing the diversity-stability relationship demonstrates a more multicausal relationship than has been previously acknowledged.

158 The relationship between the biodiversity and the stability of ecosystems has long been a
159 fundamental subject of ecological research[1–4]. More recently, this research topic has gained
160 new impetus due to concerns about the consequences of global environmental change and
161 biodiversity loss, both of which threaten the stability of ecosystem functions and the
162 ecosystem services they underpin[5–8]. Much of this work has examined the relationship
163 between plant species diversity and biomass production, often in grasslands. Both theoretical
164 and empirical research has consistently demonstrated that the primary productivity of
165 species-rich communities shows lower variation over time than that of less diverse
166 communities, a finding that has been attributed to a wide range of non-exclusive
167 mechanisms[9–16].
168
169 Temporal stability (or invariability) of ecosystem functioning is an integrative measure of the
170 responses of populations and communities to each other and to environmental variation[17].
171 While there are many means of measuring stability[8,18], temporal stability of primary biomass
172 production is typically defined as mean biomass divided by its temporal standard deviation
173 (μ/σ[19]), and it is this invariability measure that we use throughout this paper. Thus, the higher
174 stability of species-rich ecosystems is related to several properties including
175 their greater biomass, higher resistance (i.e., biomass shows little deviation from average
176 levels during perturbations) and/or resilience (i.e., biomass returns to average levels rapidly
177 after perturbations)[3,20,21]. Furthermore, numerous statistical mechanisms have been proposed
178 as drivers of stability and tested empirically[11,13,14]. Of these, perhaps the primary mechanism
179 through which diversity stabilizes biomass production is species asynchrony[13,14,22,23], which
180 describes the extent to which species-level productivity is correlated within a community
181 over time. Asynchrony, where decreases in the productivity of some species are compensated
182 by increases in the productivity of other species, can promote ecosystem stability as a

183 consequence of interspecific interactions[14,24], negative frequency dependence, e.g. due to
184 pathogen outbreaks[25,26], and/or the greater likelihood that diverse communities contain a
185 wider range of species' responses to environmental conditions[13,27]. Accordingly, it is likely
186 that multiple and correlated facets of biodiversity[28] underpin species asynchrony, including
187 taxonomic diversity[29], functional diversity[30,31], and phylogenetic diversity[32], which
188 collectively may influence ecosystem stability[33–35]. We hypothesize that the relationship
189 between biodiversity and ecosystem stability is mediated by four classes of biological drivers
190 and that these operate both directly, e.g. by affecting biomass production, and indirectly, via
191 species asynchrony.
192
193 The first class of biological drivers is functional composition, which may stabilize biomass
194 production in grasslands because growth-related traits strongly influence the production,
195 persistence, and stability of plant biomass[36]. While plants differ greatly in their trait values
196 and strategies, a large proportion of global plant trait variation is correlated along a single leaf
197 economics axis that distinguishes between exploitative species that are capable of rapid
198 resource uptake, growth, and tissue turnover (hereafter 'fast' species) and conservative
199 species with slower rates of growth, resource uptake, and tissue turnover (hereafter 'slow'
200 species[37,38]). The former typically possess high specific leaf area (SLA), low leaf dry matter
201 content (LDMC), and high leaf nitrogen concentrations (N), the latter the opposite[38–40]. There
202 is growing evidence that variation in functional composition along this 'fast-slow' leaf
203 economics spectrum influences ecosystem stability. For example, communities dominated by
204 species with high LDMC values have been found to increase ecosystem stability in
205 experimental and semi-natural grassland communities[41]. As high ecosystem resistance may
206 limit the capacity for high resilience to be expressed by preventing perturbations from
207 affecting baseline conditions, we may therefore expect that communities dominated by

208 species with slow leaf economics ('slow communities') will be more stable than those
209 dominated by species with fast leaf economics ('fast communities')[42]. However, the net effect
210 of fast-slow functional composition on ecosystem stability across multiple communities may
211 be low because the opposing effects of fast communities, which should be more resilient, and
212 slow communities, which should be more resistant, may cancel each other out.
213
214 Variation in fast-slow plant ecological strategies within a community, which can be
215 quantified using functional diversity metrics, is the second class of biological drivers that
216 may explain ecosystem stability. As fast species are likely to recover rapidly following
217 disturbance (resilience), and slow species will be better able to tolerate environmental
218 stresses and perturbations (resistance[38,39]), we hypothesize that communities with a diversity
219 of fast-slow traits will exhibit both greater resistance and higher resilience, thus increasing
220 ecosystem stability.
221
222 The third class of biological drivers that we propose as underlying the diversity-stability
223 relationship are those associated with phylogenetic diversity. Generally, phylogenetic
224 diversity can be seen as representing the diversity of phylogenetically conserved functional
225 traits, which may constitute a broader set of traits than is typically included in functional
226 diversity measures. Traits that reflect a shared co-evolutionary history of biotic interactions
227 often show a high degree of phylogenetic conservatism[43], such as symbiotic N_2 fixation and
228 mycorrhizal tendency[33,44]. Closely related species are also known to share pathogens or
229 immune responses via their shared co-evolutionary history[45,46]. Importantly, phylogenetic
230 diversity has been shown to positively affect ecosystem stability in grasslands in most
231 analyses[32,33,35], but not all[29]. We therefore hypothesize that greater phylogenetic diversity will
232 stabilize biomass production over time by increasing (measured and unmeasured) trait

diversity and by diluting the effects of pathogen outbreaks and herbivore attacks, which are strong regulators of biomass production in grasslands[46].

Finally, plant species richness may affect ecosystem stability via pathways that are trait-based but not associated with the leaf economics spectrum and not phylogenetically conserved. This class of mechanism may include the effects of persistent seedbanks[47], regrowth from belowground storage organs[48], carbohydrate reserves[49], variation in rooting depth[50], and phenology[51]. We expect that these effects will indirectly enhance ecosystem stability via increased asynchrony[13] and directly via greater mean biomass production over time[29,52].

While there is empirical evidence, typically from single sites, that each of the aforementioned biological drivers contributes to the overall relationship between diversity and stability, they likely operate concurrently and their relative importance and interrelationships have not been investigated. Here, we make a general, integrative assessment of the contribution of different facets of biodiversity in driving biodiversity-stability relationships. This was achieved by performing a meta-level analysis using data from 39 grassland biodiversity-ecosystem function experiments distributed across North America and Europe. Direct and indirect effects of the biological drivers were assessed using structural equation models (SEM), which represented the relationships described above (Supplementary Figs. 1 & 2), and which control for covariation among the different facets of biodiversity[29,35]. We hypothesized that: *i*) greater plant species richness, diversity in traits that capture the fast-slow leaf economics spectrum, and phylogenetic diversity will increase ecosystem stability by increasing asynchrony and that *ii*) species-rich communities with high fast-slow functional diversity and phylogenetic diversity, and those dominated by species with slow leaf economics, will increase ecosystem stability directly as they increase the temporal mean of biomass production, a component of

stability, via classical diversity-function mechanisms, e.g. complementarity and selection effects[24,53].

Results

Our analysis shows positive bivariate relationships between stability, asynchrony and several biodiversity facets: species richness, phylogenetic diversity (calculated as mean nearest taxon distance, MNTD, see Methods), fast-slow functional diversity (calculated using traits associated with the fast-slow leaf economics spectrum), and that these are significant and generally consistent across experiments (Figs. 1 & 2). These drivers explained low amounts of variation in ecosystem stability (Supplementary Table 1, marginal R^2), with a larger proportion being explained by the random effects (Supplementary Tables 1 and 2, conditional R^2). In contrast, although phylogenetic diversity and fast-slow functional diversity were positively related to ecosystem stability, there was no consistent effect of the community-weighted mean of fast-slow traits on ecosystem stability ($P > 0.10$; Fig. 2c). However, the effect of the community-weighted mean of fast-slow traits was highly variable across all experimental sites; at certain experimental sites dominance by species with slow traits stabilized productivity (Fig. 2c), while fast species stabilized production at others.

These relationships were investigated in more depth with our structural equation model, which provides strong evidence that asynchrony is a key mechanism mediating the biodiversity-stability relationship and that asynchrony is driven by multiple facets of biodiversity (Fig. 3). Overall, the data fit our model well (Fisher's $C = 7.51$, $df = 12$, $P = 0.82$; $K = 34$, $n = 1{,}699$). Fixed effects explained 20% of variation in ecosystem stability (marginal R^2), which increased to 59% (conditional R^2) when accounting for fixed and random effects. In total, plant species richness, phylogenetic diversity, fast-slow functional

283 diversity, and mean and inter-annual variation in water availability explained 52% of
284 variation in species asynchrony (marginal R^2), which increased to 79% when random effects
285 were accounted for (conditional R^2).
286
287 The strongest pathway of influence on ecosystem stability was from plant species richness
288 via species asynchrony (standardized path coefficient of indirect effect = 0.21). This effect
289 was larger and more consistent across experimental sites than the direct effect of species
290 richness (standardized path coefficient of direct effect = 0.03, P = 0.60), thus suggesting that
291 much of the effect of plant species richness on ecosystem stability is explained by species
292 asynchrony. Phylogenetic diversity also had strong yet opposing effects on ecosystem
293 stability. It indirectly increased ecosystem stability via asynchrony (standardized path
294 coefficient of indirect effect = 0.12), while the direct pathway between phylogenetic diversity
295 and ecosystem stability was negative (standardized path coefficient of direct effect = - 0.10; P
296 < 0.001). This negative effect was weaker than the positive indirect effect via species
297 asynchrony, thus explaining the overall positive relationship between phylogenetic diversity
298 and ecosystem stability, along with covariance with species richness (Fig. 2a).
299
300 The community-weighted mean of fast-slow traits had a direct negative effect on ecosystem
301 stability, meaning that communities dominated by slow species were more stable than those
302 dominated by fast species (Fig. 3). Contrary to our expectations, the SEM revealed that fast-
303 slow functional diversity did not directly or indirectly (via asynchrony) stabilize ecosystem
304 productivity (P > 0.05). Furthermore, these weak effects of fast-slow functional diversity on
305 ecosystem stability were also generally robust to the use of an alternative measure of fast-
306 slow functional diversity, functional richness (Supplementary Fig. 3). Finally, we assessed
307 potentially important effects of climate and found that mean and inter-annual variation in

water availability had significant, yet opposite effects on ecosystem stability and no significant effects on species asynchrony (Fig. 3).

Further analyses provided added insight into mechanisms underlying the biodiversity-stability relationship. By including the two components of the invariability measure in a separate SEM, i.e., mean and standard deviation of biomass production, we found that species richness and the community-weighted mean of fast-slow traits stabilized mean aboveground biomass production while asynchrony decreased inter-annual variation in biomass (Fig. 4; Fisher's C = 22.19, df = 22, P = 0.45; K = 49, n = 1,699). Fixed effects explained 52% of variation in ecosystem stability (marginal R^2), which increased to 64% (conditional R^2) when also accounting for random effects. Multiple facets of biodiversity and climate only explained 15% and 8% of variation in mean and standard deviation of biomass production (marginal R^2), respectively. When also accounting for across-site variation (conditional R^2), explained variation increased to 66% for mean aboveground biomass production and 48% for the standard deviation of biomass.

Species richness promoted ecosystem stability by increasing mean aboveground biomass production but also increasing its variability, while the direct effect of phylogenetic diversity on ecosystem stability operated via negative effects on the standard deviation of biomass. Furthermore, these analyses revealed that the weak negative effect of the community-weighted mean of fast-slow traits on ecosystem stability masked contrasting effects on the components of the invariability measure; communities dominated by species with fast trait values decreased mean biomass (standardized path coefficient of direct effect = -0.12) to a greater extent than they decreased standard deviation of biomass (standardized path coefficient of direct effect = -0.08). Asynchrony increased ecosystem stability by reducing

333 the standard deviation of biomass. Finally, inter-annual variation in water availability had
334 strong yet variable effects on the standard deviation of biomass (standardized path coefficient
335 of direct effect = 0.17, P = 0.08), while those of mean water availability on mean
336 aboveground biomass production were weak. These relationships were generally robust to the
337 use of different combinations of phylogenetic and functional diversity indices and detrended
338 ecosystem stability (Supplementary Figs. 4-8).
339
340 As most studies available for inclusion in our analyses collected data for less than four years
341 (33 of 39 studies), we performed sensitivity analyses to test whether our results differed
342 between short- and long-term studies. We found that bivariate relationships between stability
343 and individual facets of biodiversity had similar results between short- and long-term studies,
344 as indicated by non-significant interactions between study duration and each facet of
345 biodiversity (Supplementary Table 3). In an SEM using only data from long-term studies (six
346 studies >4 years, n = 454 plots), we found that our overall conclusions were not affected by
347 study duration but that certain paths became stronger, with notable increases in the effects of
348 fast-slow functional diversity (Supplementary Fig. 9). In long-term studies, fast-slow
349 functional diversity had both a direct positive effect on ecosystem stability and a negative
350 effect operating on asynchrony (Supplementary Fig. 9). The strength of the effects of the
351 community-weighted mean of fast-slow traits on ecosystem stability also increased, with fast
352 communities having a direct negative effect on ecosystem stability (Supplementary Fig. 9).
353 Further sensitivity analyses showed that trait identity affected path strength and direction
354 (Supplementary Figs. 10-13). Of the four individual traits making up the fast-slow leaf
355 economics spectrum, the community-weighted means of leaf P and leaf N had direct positive
356 and negative effects on ecosystem stability, respectively, while the effects of the community-
357 weighted means of LDMC and SLA on ecosystem stability were not statistically significant.

Discussion

The results support our overall hypothesis that multiple facets of biodiversity mediate the diversity-stability relationship, principally via their effects on species asynchrony. However, the relative importance of certain biological drivers, e.g. community-weighted mean of fast-slow leaf traits, varied substantially across studies.

The strongest and most consistent driver of stability across the 39 experiments examined in our study was that of species richness, operating via species asynchrony. This likely reflects niche differences among species that affect their relative performance over time in a temporally variable environment[22,54–56]. However, these niche differences were not captured by the functional diversity of fast-slow leaf traits or phylogenetic diversity. Instead, the species richness-asynchrony-stability relationship may be driven by unmeasured traits that are not phylogenetically conserved. Such traits may be related to rooting strategies, photosynthetic pathways, non-structural carbohydrate concentrations, and properties related to phenology, demographic storage and regeneration[48,49,51,57–59]. Data for some of these traits is relatively sparse[60] and the collection of such information should be a priority in addressing the current question and those related to other aspects of ecosystem stability, i.e. resistance and resilience[61].

Species richness also affected ecosystem stability directly. We found that species richness stabilizes biomass production via its stronger effects on mean biomass production over time than effects operating via the standard deviation, which is in line with previous studies[14,29]. As with the effects of species richness on asynchrony, we suggest that these effects may be explained by effects of species richness on complementarity and selection[24,53] that are

384 unrelated to the functional diversity of fast-slow leaf traits or phylogenetic diversity.

385

386 The next most important driver of diversity-stability relationships was phylogenetic diversity.
387 Interestingly, phylogenetic diversity influences ecosystem stability via two different
388 pathways, one positive and operating indirectly via species asynchrony, and one negative and
389 operating directly. The indirect asynchrony pathway was the stronger of the two, resulting in
390 a positive overall effect and is likely due to a range of phylogenetically conserved traits. As
391 herbivores and pathogens often have a narrow and phylogenetically conserved host range[45,46],
392 herbivore attacks and disease outbreaks can be weaker in communities of distantly related
393 species and thus affect only a small proportion of community biomass. In contrast,
394 phylogenetically clustered communities will experience strong and simultaneous reductions
395 in biomass production as pests and pathogens spread across the community. The weaker
396 direct negative effect operated via standard deviation in biomass. This path may reflect
397 experimental communities that are dominated by more inherently stable and phylogenetically
398 clustered plant functional groups, such as grasses[62,63]. Furthermore, our analysis illustrates
399 that the effects of phylogenetic diversity on ecosystem stability are sensitive to the
400 phylogenetic diversity metric used[35]. Consistent with [29], but in contrast with those presented
401 in Figs. 3 and 4, SEMs using mean pairwise distance (MPD) showed weak direct and indirect
402 effects of phylogenetic diversity on ecosystem stability, probably due to its strong, positive
403 correlation with plant species richness (Supplementary Figs. 3 & 4, Supplementary Appendix
404 2). We suggest that the stronger effects of MNTD reflect the fact that it better represents the
405 tendency for pathogens and herbivores, which play a major role in driving grassland
406 productivity[25,64], to have a phylogenetically narrow host range[45,46].

407

408 Evidence for the fast-slow leaf economics spectrum affecting ecosystem stability as an

409 overall strategy (community-weighted mean) was weak across the full dataset. However, this
410 relationship masked contrasting effects of fast traits, which reduced mean aboveground
411 biomass production while reducing its standard deviation. The net result was that
412 communities dominated by species with fast trait values were marginally less stable than
413 those dominated by species with slow trait values. Furthermore, individual site-level
414 relationships between the community-weighted mean of fast-slow traits and ecosystem
415 stability were often very strong, but extremely variable across sites. These findings suggest
416 that the relationship between the fast-slow leaf economics spectrum and ecosystem stability is
417 heavily dependent upon site-specific factors, which could include study duration,
418 environmental conditions, and the 'matching' of appropriate functional strategies to a site.
419 For example, fast traits may confer ecosystem stability at sites subject to repeated
420 disturbances due to their ability to allow fast recovery, while slow traits may confer
421 ecosystem stability in the face of chronic environmental stresses, such as low nutrient
422 availability or water availability, e.g. the Texan dry grasslands included in our study[65,66]. Site-
423 level information detailing disturbance regimes and the constancy of soil water availability
424 and nutrient supply at a finer temporal resolution may clarify in which environmental
425 conditions particular plant strategies stabilize (or destabilize) biomass production[67].
426
427 The effect of fast-slow functional diversity and the community-weighted mean of fast-slow
428 traits became markedly stronger when only long-term (i.e. >4 year) studies were considered.
429 We hypothesize that this is due to the strengthening of biodiversity effects on mean
430 community biomass production over time[68]. Furthermore, the hypothesized effects of fast and
431 slow traits on resilience and resistance have a greater chance of detection because extreme
432 events, e.g. drought, are more likely to occur in long-term studies[21]. However, such patterns
433 may also be driven by ecological differences in the sites where long- and short-term studies

434 were conducted, as long-term sites tended to include more communities dominated by slow
435 species (Supplementary Fig. 14).
436
437 The final driver of ecosystem stability in our models was climate. Mean and inter-annual
438 variation in water availability had equally strong, yet opposing effects on ecosystem stability,
439 which were manifested largely via the standard deviation of aboveground biomass production
440 over time. This is likely to represent the strong annual variation in the timing and intensity of
441 aboveground biomass production in seasonal environments, e.g. inter-annual variation in
442 temperature and the timing and intensity of rains, and provides evidence that inter-annual
443 climatic variability may be a key driver of ecosystem stability[67,69,70]. As mentioned above, a
444 better characterization of site conditions may provide a more complete understanding of the
445 drivers of ecosystem stability[4]. Furthermore, other studies have indicated a powerful
446 interactive role between environmental conditions and biotic community properties[71,72], as
447 abiotic and management factors not only control diversity and productivity, but also influence
448 the capacity for diversity to stabilize ecosystem function by altering the mechanisms that
449 regulate diversity, such as asynchrony and resource-use complementarity[23,67,73]. This means
450 that under natural conditions changes in diversity are not the ultimate cause of ecosystem
451 stability, but are an intermediate property of ecosystem response to global change drivers that
452 might also influence ecosystem stability via other pathways. A greater understanding of these
453 interactions and how they operate in natural ecosystems is required to improve both our
454 fundamental understanding of ecosystem stability and to integrate knowledge of diversity-
455 stability relationship into agroecosystem management[74]. To do this, further studies that
456 incorporate both global change drivers, and the measurement and manipulation of diversity
457 are required[75,76]. Threshold-based measures of stability[17] may also be more relevant to
458 agroecological research than the variability measures employed here, as such measures allow

459 under- and overproduction to be considered differently.

460

461 In conclusion, our study makes a general, multi-site assessment of how multiple facets of
462 biodiversity, e.g. taxonomic, functional, and phylogenetic diversity, influence diversity-
463 stability relationships. By integrating multiple factors that are hypothesized to control
464 diversity-stability relationships in a single analysis, we were able to identify several
465 important pathways, including those related to phylogenetic diversity and the fast-slow leaf
466 economics spectrum, through which plant community properties affect the stability of
467 grassland biomass productivity. Furthermore, the meta-level approach here allows us to
468 assess which of these relationships are general and strong, and which are context dependent.
469 In an era of increased climatic variability[77,78] and biodiversity change, it is important to gain a
470 deeper understanding of each of these component processes so that the functional benefits of
471 biodiversity may be effectively conserved and promoted.

472

473 **Methods**

474 **Data preparation**

475 We assembled a database by combining data from biodiversity experiments that manipulated
476 plant species richness in grasslands and measured community- and species-level aboveground
477 plant biomass annually for at least three years. In total, we used data from 39 studies across
478 North America and Europe (Supplementary Table 4) from [21] and [73]. Our dataset comprises
479 observations from 1,699 plots and 165 plant species, which were standardized using the
480 Taxonomic Name Resolution Service (http://trns.iplantcollaborative.org[79]).

481

482 For each plot within the experiments, we quantified ecosystem stability as the inverse of the
483 coefficient of variation of aboveground plant biomass (μ/σ[19]), which is the ratio of the mean

484 to the standard deviation of annual aboveground plant biomass over time. Ecosystem stability
485 was determined with and without detrending, as recent studies have shown directional
486 changes in aboveground plant biomass with time[52,68]. Ecosystem stability was detrended by
487 regressing aboveground plant biomass against experimental year and calculating the standard
488 deviation of the residuals of each regression[9]. For each plot, detrended ecosystem stability
489 was calculated as mean aboveground plant biomass divided by the detrended standard
490 deviation. All main analyses were performed using ecosystem stability with (Figs. 1-4) and
491 without detrending (Supplementary Figs. 5-8). As results were qualitatively similar, we
492 present results for ecosystem stability without detrending in the main text and for detrended
493 ecosystem stability in Supplementary Information .
494
495 Following [14], species synchrony (η) was quantified as the average correlation across species
496 between the biomass of each species and the total biomass of all other species in a plot:
497 $\eta = (1/n) \Sigma_i \text{ corr } (Y_i, \Sigma\, j \neq i\ Y_j)$, (1)
498 where Y_i is the biomass of species *i* in a plot containing *n* species. Because asynchrony
499 implies negative synchrony, we multiplied η by -1. Thus, species asynchrony (-η) ranges
500 from -1, where species' aboveground plant biomass is maximally synchronous, to 1, where
501 species' aboveground plant biomass is maximally asynchronous. Further, -η is independent of
502 the number of species and their individual variances[14], which contrasts with species
503 asynchrony as calculated by [80].
504
505 We selected four leaf traits associated with the fast-slow leaf economics spectrum[37], specific
506 leaf area (SLA; $mm^2\ mg^{-1}$), leaf dry matter content (LDMC; $g\ g^{-1}$), foliar N (%), and foliar P
507 (%). These data were obtained from the TRY database[81] (Supplementary Appendix 1) and
508 additional studies in our database that measured traits[82–85]. Trait values were converted to

509 standardized units and those considered unlikely to be correct (z-score > 4[81]) were excluded.
510 Values were then averaged by trait data contributor and then by species. Genus-level means
511 were used when species-level data were not available; species-level data for SLA, LDMC,
512 leaf N, and leaf P were available for 98%, 83 %, 92 %, and 62 % of species, respectively.
513 Combining species- and genus-level values, our final trait data set included SLA, LDMC, and
514 foliar N values for more than 96% of the species and leaf P values for 93% of the species.
515 While absolute values of species-level traits may differ between locally collected data and
516 databases, which may influence our ability to detect biodiversity effects[86], inter-specific
517 variation is usually greater than intra-specific variation (particularly for organ-level traits)
518 and species ranking is conserved for commonly used traits across data sources[87,88].
519
520 **Fast-slow functional composition and diversity**
521 We used the first axis of a principal component analysis (PCA) of community-weighted
522 means of SLA, LDMC, leaf N, and leaf P to represent the fast-slow leaf economics spectrum
523 (hereafter 'community-weighted mean (CWM) of fast-slow traits[38]). PCA was performed
524 using the *PCA* function in 'FactoMineR'[89]. The first PCA captured 60.4% of variation among
525 the four traits (Supplementary Fig. 15) and represents the fast-slow leaf economics spectrum
526 of communities, from those dominated by slow species with low SLA and leaf N and P and
527 high LDMC to those dominated by fast species with high SLA and leaf N and P and low
528 LDMC.
529
530 We calculated functional diversity in traits associated with the fast-slow leaf economics
531 spectrum (hereafter 'fast-slow functional diversity') as either abundance-weighted functional
532 dispersion or functional richness to represent complementarity among co-occurring species
533 and volume of trait space, respectively, using the 'FD' package[90]. Results for both measures

of fast-slow functional diversity were qualitatively similar. Therefore, we present results for functional dispersion in the main text and for functional richness in Supplementary Information. Functional composition and functional diversity were calculated annually for each plot and then averaged across years.

Phylogenetic diversity

We used the molecular phylogeny from [91,92] as a backbone to build a phylogeny of all species within the experiments, conservatively binding species into the backbone using dating information from congeners in the tree (using *congeneric.merge*[93]). We then calculated abundance-weighted phylogenetic diversity as mean nearest taxon distance (MNTD[94]) and mean pairwise distance (MPD) annually for each plot and then calculated the average across years. MNTD has captured competitive differences among species in previous studies[95] and the sharing of specialized pathogens tends to be confined to closely related species[45,46]. MNTD, therefore, is a good metric to test our hypotheses about the mechanisms that explain variation in species asynchrony and ecosystem stability. Furthermore, there was a strong, positive correlation between MPD and plant species richness ($r = 0.86$; Supplementary Appendix 2). We therefore present results for MNTD in the main text and for MPD in Supplementary Information.

Climate

As empirical and theoretical studies have shown strong impacts of mean and inter-annual variation in water availability on productivity in grasslands[67,69,70], we included site-level climate data to explain across-site variation in ecosystem stability and species asynchrony. To capture the joint effects[96] of precipitation and temperature on experimental plant communities during each study, we calculated a water availability index as the ratio of annual precipitation

559 to potential evapotranspiration[97] using data from CRU TS 4.0.1[98] (Supplementary Table 4).
560 For each study, we calculated mean and the standard deviation of water availability.
561
562 **Data analysis**
563 To explore bivariate relationships between each of our hypothesized drivers and ecosystem
564 stability, we fit separate linear mixed-effects models (independently of SEMs) that tested for
565 the effects of plant species richness, phylogenetic diversity, fast-slow functional diversity,
566 community-weighted mean of fast-slow traits, and species asynchrony on ecosystem stability.
567 Multiple random effect structures were tested for each model, first using a basic structure
568 defined by the experimental design of all studies where study was treated as a random
569 intercept and species richness as a random slope. We also tested for interactions of predictor
570 variables with plant species richness and included them as random slopes when supported by
571 model selection. We used AICc to select the most parsimonious random effects structure.
572 AICc is a second-order bias correction to Akaike's information criterion for small sample
573 sizes[99]. Models were fit using the 'nlme' package and model assumptions were checked by
574 visually inspecting residual plots for homogeneity and quantile-quantile plots for normality.
575 Intra-class correlation (ICC) was calculated to compare variability within a study to
576 variability across studies.
577
578 Because many studies collected data for less than four years, we also tested whether our
579 results differed between short- and long-term studies. We did so by adding a two-way
580 interaction between a predictor variable and study duration and study duration as a main
581 effect to the models in Supplementary Table 1, where study duration was a binary variable
582 with a value of one for studies that collected data for more than four years and a value of zero
583 for all other studies. For all models, we found similar results between short- and long-term

584 studies, as interactions between each facet of biodiversity and study duration were not
585 statistically significant (Supplementary Table 3).
586
587 To test the relative importance of the different mechanisms represented by the community-
588 weighted mean of fast-slow traits, fast-slow functional diversity, phylogenetic diversity,
589 climate, and asynchrony in driving temporal stability, we fit piecewise structural equation
590 models[100] (SEM) using 'piecewiseSEM'. Testing for relationships with resistance and
591 resilience (as in [21]) was not possible because of the unequal distribution of extreme climate
592 events across sites, which prevented fitting a general SEM. We formulated a hypothetical
593 causal model (Supplementary Fig. 1) based on *a priori* knowledge of grassland ecosystems
594 and used this to test the fit of the model to the data. We also included direct paths from
595 species richness, fast-slow functional diversity, and phylogenetic diversity to ecosystem
596 stability to represent biological drivers that influence ecosystem stability, e.g. via
597 complementarity effects on the temporal mean of biomass production[24,53]. Finally, we
598 included direct paths from mean and inter-annual variation in water availability to ecosystem
599 stability. We included direct paths from species richness to fast-slow functional diversity and
600 phylogenetic diversity because variation in these variables can be directly attributed to the
601 experimental manipulation of species richness in all studies[33].
602
603 All initial models contained partial bivariate correlations between fast-slow functional
604 diversity and phylogenetic diversity[35]. Additional partial bivariate correlations were added to
605 the initial model if they significantly improved model fit using modification indices ($P < 0.05$).
606 To test the sensitivity of our model to functional and phylogenetic diversity indices, the
607 duration of the time series, and the choice of traits, we fit additional models for each
608 combination of functional and phylogenetic diversity indices, using only data from long-term

experiments (>4 years), and for each functional trait separately. Finally, we fit another SEM to see if stabilizing effects on biomass production operated via the two components of the invariability measure, mean and standard deviation of biomass production (Supplementary Fig. 2). In this model, we added direct paths from species richness, phylogenetic diversity, fast-slow functional diversity, and species asynchrony to the mean and standard deviation of biomass and from mean water availability to mean biomass and from inter-annual variation in water availability to standard deviation of biomass production. Model fit was assessed using Fisher's C statistic ($P > 0.10$). SEMs were fit using linear mixed-effects models where study was treated as a random factor and species richness as a random slope. Random effect structures allowed the intercepts and slopes to vary among studies. In all analyses, plant species richness,ecosystem stability, and mean water availability were $\log_2$ transformed to meet normality assumptions. Model assumptions of normality were inspected visually. As many of the variables included in our SEM were correlated (see Supplementary Appendix 2), we estimated variance inflation. This demonstrated that multi-collinearity did not affect parameter estimates (VIF < 3). All analyses were performed using R 3.4.4[101].

Data availability. Data supporting the findings of this study are available from the authors upon request.

Code availability. R code of all analyses is available via GitHub (https://github.com/idiv-biodiversity/StabilityII).

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635 **References**

1. May, R. M. *Stability and complexity in model ecosystems*. **6,** (Princeton University Press, 1973).
2. McNaughton, S. J. Stability and diversity of ecological communities. *Nature* **274,** 251–253 (1978).
3. Tilman, D. & Downing, J. A. Biodiversity and stability in grasslands. *Nature* **367,** 363–365 (1994).
4. Ives, A. R. & Carpenter, S. R. Stability and Diversity of Ecosystems. *Science* **317,** 58–62 (2007).
5. Balvanera, P. *et al.* Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* **9,** 1146–1156 (2006).
6. Hautier, Y. *et al.* Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science* **348,** 336–340 (2015).
7. Isbell, F., Tilman, D., Polasky, S. & Loreau, M. The biodiversity-dependent ecosystem service debt. *Ecol. Lett.* **18,** 119–134 (2015).
8. Donohue, I. *et al.* Navigating the complexity of ecological stability. *Ecol. Lett.* **19,** 1172–1185 (2016).
9. Tilman, D., Reich, P. B. & Knops, J. M. H. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441,** 629–632 (2006).
10. Jiang, L. & Pu, Z. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *Am. Nat.* **174,** 651–659 (2009).
11. Hector, A. *et al.* General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* **91,** 2213–2220 (2010).
12. Campbell, V., Murphy, G. & Romanuk, T. N. Experimental design and the outcome and interpretation of diversity–stability relations. *Oikos* **120,** 399–408 (2011).
13. de Mazancourt, C. *et al.* Predicting ecosystem stability from community composition and biodiversity. *Ecol. Lett.* **16,** 617–625 (2013).
14. Gross, K. *et al.* Species Richness and the Temporal Stability of Biomass Production: A

New Analysis of Recent Biodiversity Experiments. *Am. Nat.* **183,** 1–12 (2014).

15. Aussenac, R. *et al.* Intraspecific variability in growth response to environmental fluctuations modulates the stabilizing effect of species diversity on forest growth. *J. Ecol.* **105,** 1010–1020 (2017).
16. del Río, M. *et al.* Species interactions increase the temporal stability of community productivity in Pinus sylvestris–Fagus sylvatica mixtures across Europe. *J. Ecol.* **105,** 1032–1043 (2017).
17. Oliver, T. H. *et al.* Biodiversity and Resilience of Ecosystem Functions. *Trends Ecol. Evol.* **30,** 673–684 (2015).
18. Arnoldi, J.-F., Loreau, M. & Haegeman, B. Resilience, reactivity and variability: a mathematical comparison of ecological stability measures. *J. Theor. Biol.* **389,** 47–59 (2016).
19. Tilman, D. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80,** 1455–1474 (1999).
20. Van Ruijven, J. & Berendse, F. Diversity enhances community recovery, but not resistance, after drought. *J. Ecol.* **98,** 81–86 (2010).
21. Isbell, F. *et al.* Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526,** 574–577 (2015).
22. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proc. Natl. Acad. Sci.* **96,** 1463–1468 (1999).
23. Hautier, Y. *et al.* Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* **508,** 521–525 (2014).
24. Lehman, C. L. & Tilman, D. Biodiversity, Stability, and Productivity in Competitive Communities. *Am. Nat.* **156,** 534–552 (2000).
25. Maron, J. L., Marler, M., Klironomos, J. N. & Cleveland, C. C. Soil fungal pathogens and the relationship between plant diversity and productivity. *Ecol. Lett.* **14,** 36–41 (2011).
26. Schnitzer, S. A. *et al.* Soil microbes drive the classic plant diversity–productivity pattern. *Ecology* **92,** 296–303 (2011).

27. Tredennick, A. T., de Mazancourt, C., Loreau, M. & Adler, P. B. Environmental responses, not species interactions, determine synchrony of dominant species in semiarid grasslands. *Ecology* **98,** 971–981 (2017).
28. Naeem, S. *et al.* Biodiversity as a multidimensional construct: a review, framework and case study of herbivory's impact on plant biodiversity. *Proc R Soc B* **283,** 20153005 (2016).
29. Venail, P. *et al.* Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. *Funct. Ecol.* **29,** 615–626 (2015).
30. Roscher, C. *et al.* Identifying population- and community-level mechanisms of diversity–stability relationships in experimental grasslands. *J. Ecol.* **99,** 1460–1469 (2011).
31. Lepš, J., Májeková, M., Vítová, A., Doležal, J. & de Bello, F. Stabilizing effects in temporal fluctuations: management, traits, and species richness in high-diversity communities. *Ecology* **99,** 360–371 (2018).
32. Cadotte, M. W., Dinnage, R. & Tilman, D. Phylogenetic diversity promotes ecosystem stability. *Ecology* **93,** S223–S233 (2012).
33. Flynn, D. F. B., Mirotchnick, N., Jain, M., Palmer, M. I. & Naeem, S. Functional and phylogenetic diversity as predictors of biodiversity-ecosystem-function relationships. *Ecology* **92,** 1573–1581 (2011).
34. Spasojevic, M. J. & Suding, K. N. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *J. Ecol.* **100,** 652–661 (2012).
35. Cadotte, M. W. Phylogenetic diversity and productivity: gauging interpretations from experiments that do not manipulate phylogenetic diversity. *Funct. Ecol.* **29,** 1603–1606 (2015).
36. Díaz, S. & Cabido, M. Vive la différence: plant functional diversity matters to ecosystem processes. *Trend Ecol. Evol.* **16,** 646–655 (2001).
37. Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428,** 821–827

(2004).

38. Reich, P. B. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *J. Ecol.* **102,** 275–301 (2014).
39. Grime, J. P. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111,** 1169–1194 (1977).
40. Díaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529,** 167–171 (2016).
41. Polley, H. W., Isbell, F. I. & Wilsey, B. J. Plant functional traits improve diversity□based predictions of temporal stability of grassland productivity. *Oikos* **122,** 1275–1282 (2013).
42. Májeková, M., de Bello, F., Doležal, J. & Lepš, J. Plant functional traits as determinants of population stability. *Ecology* **95,** 2369–2374 (2014).
43. Gomez, J. M., Verdu, M. & Perfectti, F. Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature* **465,** 918–921 (2010).
44. Reinhart, K. O., Wilson, G. W. T. & Rinella, M. J. Predicting plant responses to mycorrhizae: integrating evolutionary history and plant traits. *Ecol. Lett.* **15,** 689–695 (2012).
45. Gilbert, G. S., Magarey, R., Suiter, K. & Webb, C. O. Evolutionary tools for phytosanitary risk analysis: phylogenetic signal as a predictor of host range of plant pests and pathogens. *Evol. Appl.* **5,** 869–878 (2012).
46. Parker, I. M. *et al.* Phylogenetic structure and host abundance drive disease pressure in communities. *Nature* **520,** 542–544 (2015).
47. Pérez-Harguindeguy, N. *et al.* New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* **61,** 167–234 (2013).
48. Hoover, D. L., Knapp, A. K. & Smith, M. D. Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* **95,** 2646–2656 (2014).
49. O'Brien, M. J., Leuzinger, S., Philipson, C. D., Tay, J. & Hector, A. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nat. Clim Change* **4,** 710–714 (2014).

50. Weigelt, A., Schumacher, J., Roscher, C. & Schmid, B. Does biodiversity increase spatial stability in plant community biomass? *Ecol. Lett.* **11,** 338–347 (2008).
51. Fargione, J. & Tilman, D. Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. *Oecologia* **143,** 598–606 (2005).
52. Reich, P. B. *et al.* Impact of Biodiversity Loss Escalate Through Time As Redundancy Fades. *Science* **336,** 589–592 (2012).
53. Loreau, M. & Hector, A. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412,** 72–76 (2001).
54. Allan, E. *et al.* More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proc. Natl. Acad. Sci.* **108,** 17034–17039 (2011).
55. Isbell, F. *et al.* High plant diversity is needed to maintain ecosystem services. *Nature* **477,** 199–202 (2011).
56. Turnbull, L. A., Isbell, F., Purves, D. W., Loreau, M. & Hector, A. Understanding the value of plant diversity for ecosystem functioning through niche theory. *Proc. R. Soc. Lond. B Biol. Sci.* **283,** (2016).
57. Edwards, E. J., Osborne, C. P., Strömberg, C. A. E. & Smith, S. A. The Origins of C4 Grasslands: Integrating Evolutionary and Ecosystem Science. *Science* **328,** 587–591 (2010).
58. Bartlett, M. K., Scoffoni, C. & Sack, L. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecol. Lett.* **15,** 393–405 (2012).
59. Schroeder□Georgi, T. *et al.* From pots to plots: hierarchical trait□based prediction of plant performance in a mesic grassland. *J. Ecol.* **104,** 206–218 (2016).
60. Iversen, C. M. *et al.* A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytol.* **215,** 15–26 (2017).
61. Aubin, I. *et al.* Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. *Environ. Rev.* **24,** 164–186 (2016).

62. Hoover, D. L., Duniway, M. C. & Belnap, J. Pulse-drought atop press-drought: unexpected plant responses and implications for dryland ecosystems. *Oecologia* **179,** 1211–1221 (2015).
63. Shi, Z. *et al.* Dual mechanisms regulate ecosystem stability under decade-long warming and hay harvest. *Nat. Commun.* **7,** 11973 (2016).
64. Mitchell, C. E., Tilman, D. & Groth, J. V. Effects of Grassland Plant Species Diversity, Abundance, and Composition on Foliar Fungal Disease. *Ecology* **83,** 1713–1726 (2002).
65. Wilsey, B. J. & Polley, H. W. Realistically Low Species Evenness Does Not Alter Grassland Species-Richness-Productivity Relationships. *Ecology* **85,** 2693–2700 (2004).
66. Wilsey, B. J., Teaschner, T. B., Daneshgar, P. P., Isbell, F. I. & Polley, H. W. Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. *Ecol. Lett.* **12,** 432–442 (2009).
67. Hallett, L. M. *et al.* Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology* **95,** 1693–1700 (2014).
68. Guerrero-Ramírez, N. R. *et al.* Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nat. Ecol. Evol.* 1 (2017). doi:10.1038/s41559-017-0325-1
69. Craine, J. M. *et al.* Timing of climate variability and grassland productivity. *Proc. Natl. Acad. Sci.* **109,** 3401–3405 (2012).
70. Stuart-Haëntjens, E. *et al.* Mean annual precipitation predicts primary production resistance and resilience to extreme drought. *Sci. Total Environ.* **636,** 360–366 (2018).
71. Xu, Z. *et al.* Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony. *J. Ecol.* **103,** 1308–1316 (2015).
72. Yang, Z. *et al.* Daytime warming lowers community temporal stability by reducing the abundance of dominant, stable species. *Glob. Change Biol.* **23,** 154–163 (2017).
73. Craven, D. *et al.* Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **371,** (2016).
74. Isbell, F. *et al.* Linking the influence and dependence of people on biodiversity across scales. *Nature* **546,** 65–72 (2017).

75. Borer, E. T. *et al.* Finding generality in ecology: a model for globally distributed experiments. *Methods Ecol. Evol.* **5,** 65–73 (2014).
76. Eisenhauer Nico *et al.* Biodiversity–ecosystem function experiments reveal the mechanisms underlying the consequences of biodiversity change in real world ecosystems. *J. Veg. Sci.* **27,** 1061–1070 (2016).
77. Goodess, C. M. How is the frequency, location and severity of extreme events likely to change up to 2060? *Environ. Sci. Policy* **27, Supplement 1,** S4–S14 (2013).
78. Stott, P. How climate change affects extreme weather events. *Science* **352,** 1517–1518 (2016).
79. Boyle, B. *et al.* The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinformatics* **14,** 16 (2013).
80. Loreau, M. & Mazancourt, C. de. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat.* **172,** E48–E66 (2008).
81. Kattge, J. *et al.* TRY - a global database of plant traits. *Glob. Change Biol.* **17,** 2905–2935 (2011).
82. Grime, J. P. Plant strategy theories: a comment on Craine (2005). *J. Ecol.* **95,** 227–230 (2007).
83. Wacker, L., Baudois, O., Eichenberger-Glinz, S. & Schmid, B. Diversity effects in early- and mid-successional species pools along a nitrogen gradient. *Ecology* **90,** 637–48 (2009).
84. Roscher, C. *et al.* Using Plant Functional Traits to Explain Diversity–Productivity Relationships. *PLoS ONE* **7,** e36760 (2012).
85. Daneshgar, P. P., Polley, H. W. & Wilsey, B. J. Simple plant traits explain functional group diversity decline in novel grassland communities of Texas. *Plant Ecol.* **214,** 231–241 (2013).
86. Roscher Christiane *et al.* Origin context of trait data matters for predictions of community performance in a grassland biodiversity experiment. *Ecology* **99,** 1214–1226 (2018).

87. Kazakou, E. *et al.* Are trait-based species rankings consistent across data sets and spatial scales? *J. Veg. Sci.* **25,** 235–247 (2014).
88. Siefert, A. *et al.* A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Lett.* **18,** 1406–1419 (2015).
89. Lê, S., Josse, J., Husson, F. & others. FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* **25,** 1–18 (2008).
90. Laliberté, E. & Legendre, P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91,** 299–305 (2010).
91. Zanne, A. E. *et al.* Three keys to the radiation of angiosperms into freezing environments. *Nature* **506,** 89 (2014).
92. Zanne, A. *et al. Data from: Three keys to the radiation of angiosperms into freezing environments*. (Dryad Digital Repository, 2013). doi:10.5061/dryad.63q27.2
93. Pearse, W. D. *et al.* pez: phylogenetics for the environmental sciences. *Bioinformatics* **31,** 2888–2890 (2015).
94. Webb, C. O., Ackerly, D. D., McPeek, M. A. & Donoghue, M. J. Phylogenies and Community Ecology. *Annu. Rev. Ecol. Syst.* **33,** 475–505 (2002).
95. Godoy, O., Kraft, N. J. B. & Levine, J. M. Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.* **17,** 836–844 (2014).
96. Valencia Enrique *et al.* Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytol.* **206,** 660–671 (2015).
97. Middleton, N. J. & Thomas, D. S. *World Atlas of Desertification*. (United Nations Environment Programme / Edward Arnold, 1992).
98. Harris, I.C. & Jones, P.D. CRU TS4.01: Climatic Research Unit (CRU) Time-Series (TS) version 4.01 of high-resolution gridded data of month-by-month variation in climate (Jan. 1901- Dec. 2016). *Cent. Environ. Data Anal.*
99. Burnham, K. & Anderson, D. *Model Selection and Multimodel Inference: a practical information-theoretic approach*. (Springer Science & Business Media, 2003).
100. Lefcheck, J. S. piecewiseSEM: Piecewise structural equation modelling in r for ecology,

evolution, and systematics. *Methods Ecol. Evol.* **7,** 573–579 (2016).

101. R Core Team. *R: A Language and Environment for Statistical Computing*. (R Foundation for Statistical Computing, 2018).

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Authorship contributions

DC, NE, and FI conceived the project, DC, PM, NE, WDP, YH, CR, FI, AE, JNG, JH, AJ, NL, STM, JvR, AW, and MDS further developed the project in a workshop; NE, CR, FI, MB, CB, GB, NB, CB, BELC, JAC, JHCC, JMC, EDL, AH, AJ, JK, JK, VL, VM, VO, HWP, PBR, JvR, BS, NAS, DT, AW, and BW contributed experimental and functional trait data; DC compiled data; DC analyzed data with significant input from PM, NE, WDP, and YH. DC and PM wrote the first draft of the manuscript and all co-authors contributed substantially to revisions.

Competing interests

The authors have no competing interests.

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Figure Legends

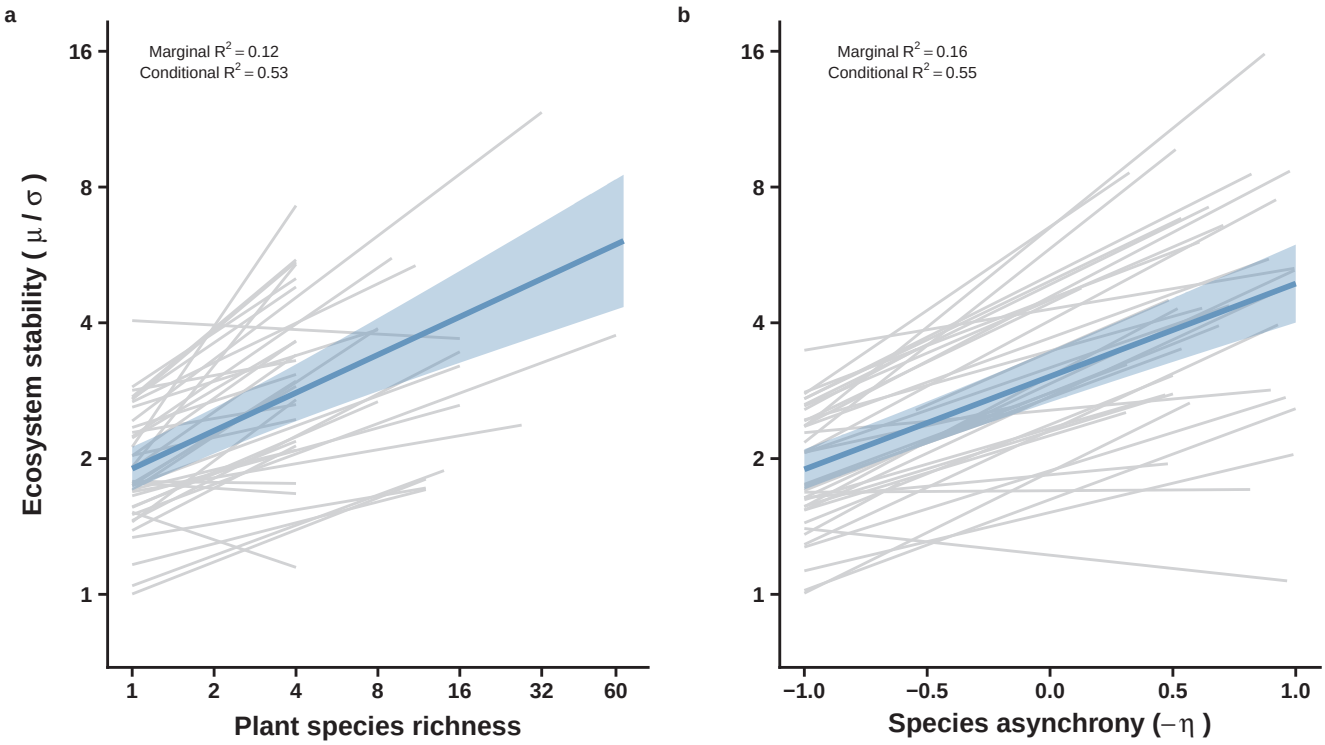
Figure 1. Plant species richness (**a**) and species asynchrony (**b**) effects on ecosystem stability of aboveground biomass production across 39 experimental grassland studies. Lines are mixed-effects model fits for each study (light gray lines) or across all studies (black lines; $P \leq 0.05$). Synchrony ranges from -1 to 1, where -1 represents maximum synchrony and +1 maximum asynchrony. Marginal and conditional R^2 represent model variation explained by fixed effects and the combination of fixed and random effects, respectively. Light blue bands represent 95% confidence intervals.

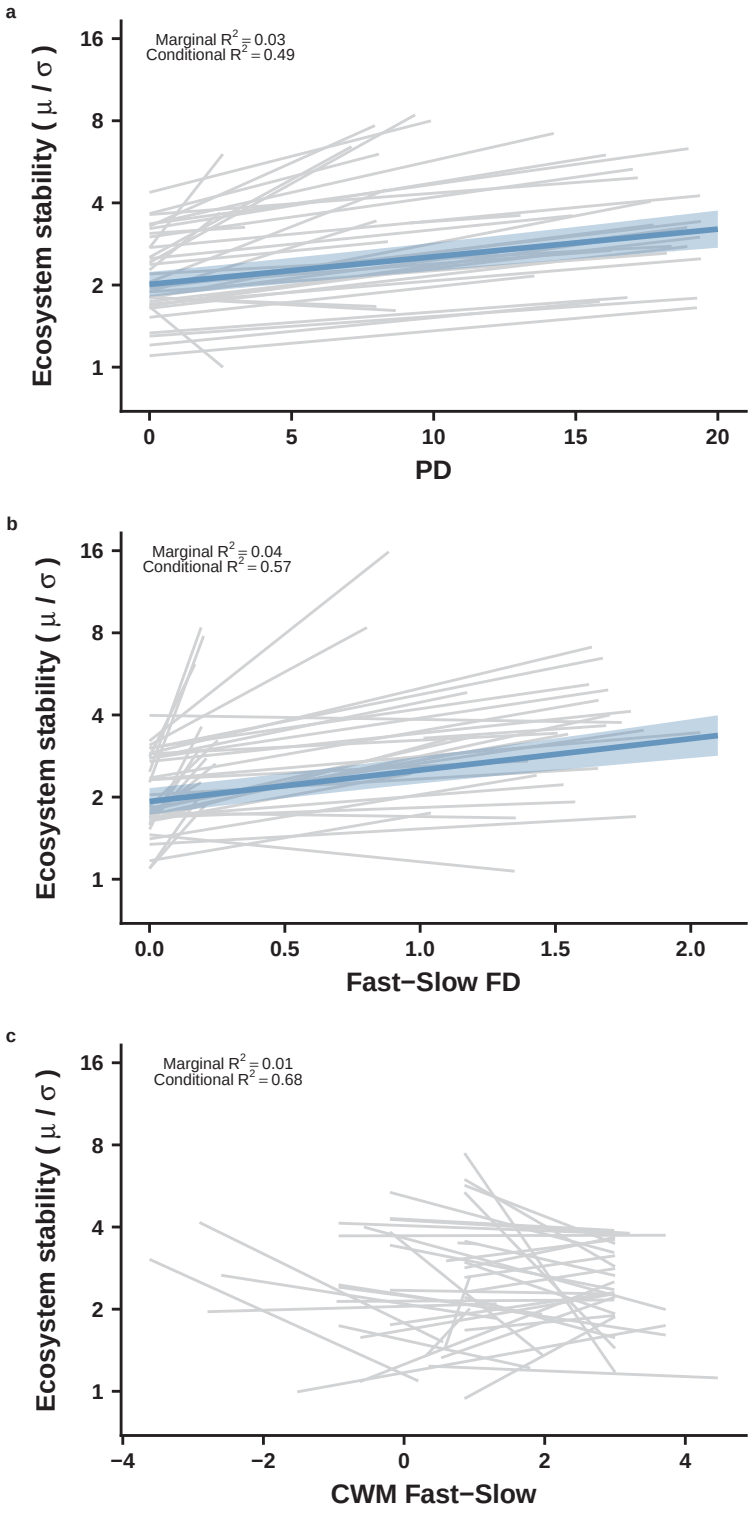
Figure 2. Phylogenetic (**a**; PD) and fast-slow functional diversity (**b;** Fast-Slow FD) and community-weighted mean of fast-slow traits (**c;** CWM Fast-Slow) effects on ecosystem stability of aboveground biomass production across 39 experimental grassland studies. Phylogenetic diversity is abundance-weighted mean nearest taxon distance (MNTD) and Fast-Slow FD is abundance-weighted functional dispersion of fast-slow traits. CWM Fast-Slow is the first axis of a principal component analysis of community-weighted means of key leaf functional traits associated with 'fast' and 'slow' ecological strategies: specific leaf area (SLA), leaf matter dry content (LMDC), and leaf N and P concentrations. Low values of the fast-slow spectrum correspond to communities dominated by 'slow' species, i.e. low SLA and leaf N and P and high LDMC and high values to communities dominated 'fast' species, i.e. high SLA and leaf N and P and low LDMC. Lines are mixed-effects model fits for each study (light gray lines) or across all studies (black lines; $P \leq 0.05$). Marginal and conditional R^2 represent model variation explained by fixed effects and the combination of fixed and random effects, respectively. Light blue bands represents 95% confidence intervals.

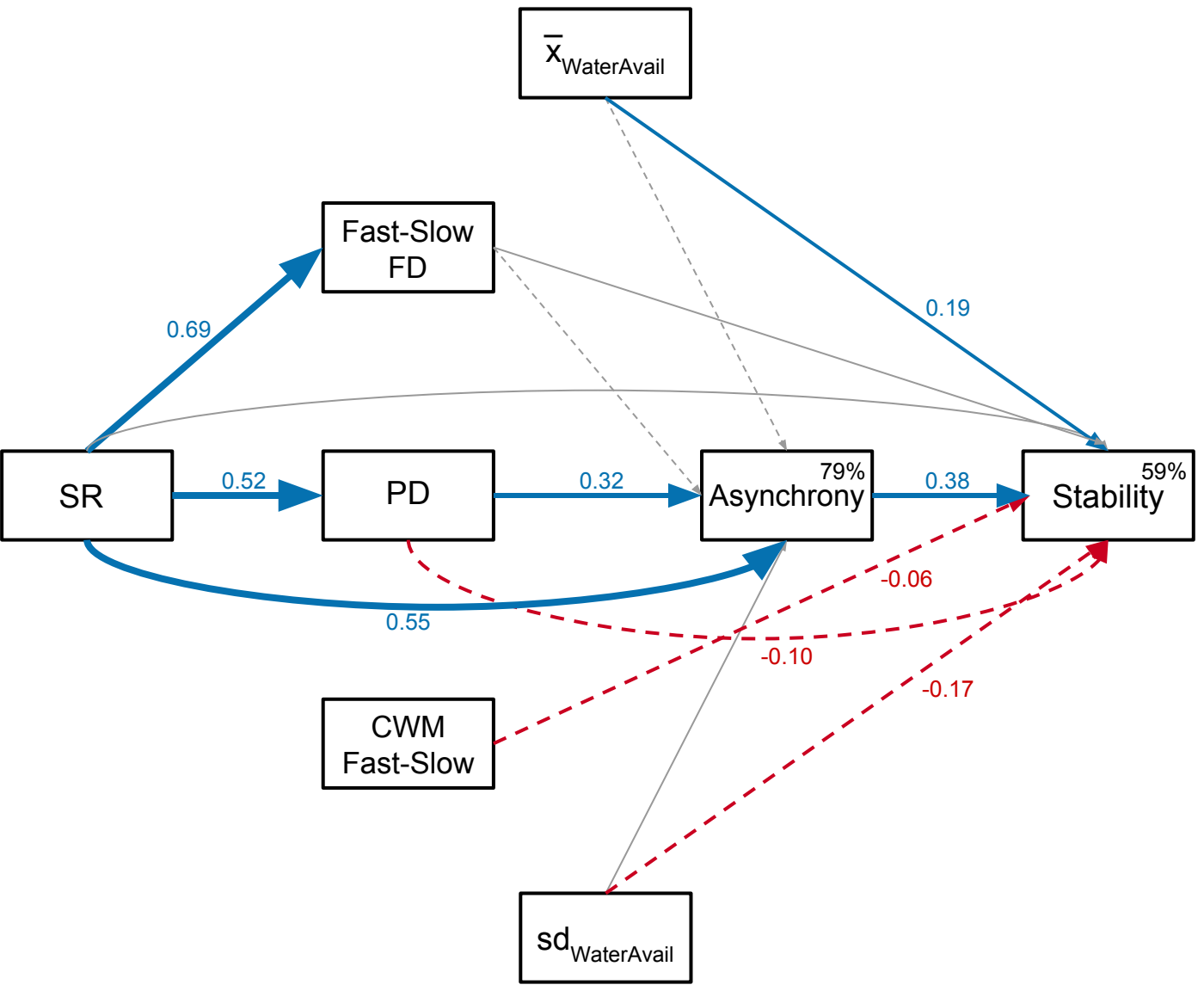
Figure 3. Structural equation model (SEM) exploring the effects of plant species richness, fast-slow functional diversity (Fast-Slow FD; abundance-weighted functional dispersion), phylogenetic diversity (abundance-weighted mean nearest taxon distance), functional composition (CWM Fast-Slow), mean ($\bar{x}_{WaterAvail}$) and inter-annual variation in water availability ($sd_{WaterAvail}$) on species asynchrony and ecosystem stability of aboveground biomass production across 39 experimental grassland studies. The model fit the data well (Fisher's $C = 7.51$, $df = 12$, $P = 0.82$; $K = 34$, $n = 1{,}699$). Boxes represent measured variables and arrows represent relationships among variables. Solid blue and dashed red arrows represent significant ($P \leq 0.05$), positive and negative standardized path coefficients, respectively, and gray arrows represent non-significant standardized path coefficients. Standardized path coefficients are given next to each (significant) path; widths of significant paths are scaled by standardized path coefficients. Conditional R^2 (based on both fixed and random effects) for asynchrony and ecosystem stability is reported in the corresponding box.

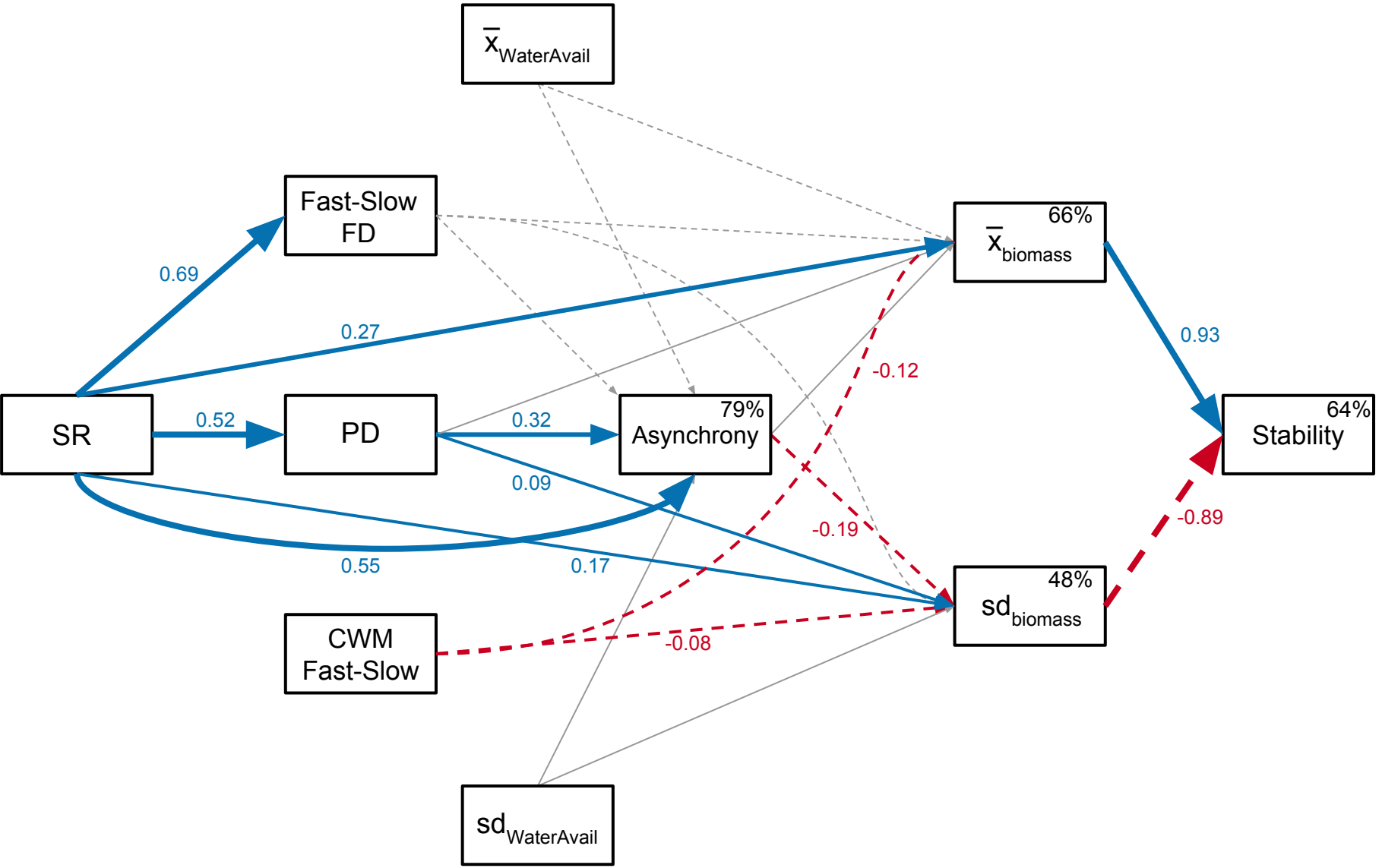
Figure 4. Structural equation model (SEM) exploring the effects of plant species richness, fast-slow functional diversity (Fast-Slow FD; abundance-weighted functional dispersion), phylogenetic diversity (abundance-weighted mean nearest taxon distance), functional composition (CWM Fast-Slow), mean ($\bar{x}_{WaterAvail}$) and inter-annual variation in water availability ($sd_{WaterAvail}$) on species asynchrony, mean ($\bar{x}_{biomass}$) and variation in ($sd_{biomass}$) aboveground biomass production and ecosystem stability of aboveground biomass production across 39 experimental grassland studies. The model fit the data well (Fisher's $C = 22.19$, $df = 22$, $P = 0.45$; $K = 49$, $n = 1{,}699$). Boxes represent measured variables and arrows represent relationships among variables. Solid blue and dashed red arrows represent significant ($P \leq 0.05$), positive and negative standardized path coefficients, respectively, and gray arrows

represent non-significant standardized path coefficients. Standardized path coefficient are given next to each (significant) path; widths of significant paths are scaled by standardized path coefficients. Conditional R^2 (based on both fixed and random effects) for asynchrony, $\bar{x}_{biomass}$, $sd_{biomass}$, and ecosystem stability is reported in the corresponding box.


a
Marginal $R^2 = 0.12$
Conditional $R^2 = 0.53$
Ecosystem stability (μ / σ)
16
8
4
2
1
1
2
4
8
16
32
60
Plant species richness
b
Marginal $R^2 = 0.16$
Conditional $R^2 = 0.55$
16
8
4
2
1
−1.0
−0.5
0.0
0.5
1.0
Species asynchrony (−η)


a
Marginal R² = 0.03
Conditional R² = 0.49
Ecosystem stability (μ / σ)
16
8
4
2
1
0
5
10
15
20
PD
b
Marginal R² = 0.04
Conditional R² = 0.57
Ecosystem stability (μ / σ)
16
8
4
2
1
0.0
0.5
1.0
1.5
2.0
Fast−Slow FD
c
Marginal R² = 0.01
Conditional R² = 0.68
Ecosystem stability (μ / σ)
16
8
4
2
1
−4
−2
0
2
4
CWM Fast−Slow


$\bar{x}_{WaterAvail}$
Fast-Slow FD
0.69
0.19
SR
0.52
PD
0.32
79%
Asynchrony
0.38
59%
Stability
0.55
-0.06
-0.10
-0.17
CWM Fast-Slow
$sd_{WaterAvail}$


$\bar{x}_{WaterAvail}$
Fast-Slow FD
0.69
0.27
SR
0.52
PD
0.32
79% Asynchrony
0.09
0.55
0.17
CWM Fast-Slow
-0.08
$sd_{WaterAvail}$
66% $\bar{x}_{biomass}$
-0.12
0.93
64% Stability
-0.19
-0.89
48% $sd_{biomass}$